Responses of Plant Communities to Incremental Hydrologic Restoration of a Tide-Restricted Salt Marsh in Southern New England (Massachusetts, U.S.A.)

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Abstract

Hydrologic restoration of Hatches Harbor, a tide-restricted marsh on Cape Cod (Massachusetts), has resulted in significant plant community changes 7 years following the reintroduction of seawater. Since 1999, incremental increases in flow through a tide-restricting dike have facilitated the rapid decline of salt-intolerant vegetation, while encouraging the expansion of native salt marsh taxa. These changes show strong spatial gradients and are correlated with marsh surface elevation, distance from the point of seawater entry, and porewater salinity. Common reed (*Phragmites australis*) has not decreased in abundance but has migrated a considerable distance up-slope. In the wake of this retreat native halophytes have proliferated. Now that maximum flow through the existing dike structure has been reached, continued recovery may be limited less by changing physicochemical conditions and more by rates of growth, seed dispersal, and seed germination of salt marsh taxa.

Key words: Cape Cod, *Phragmites*, plant community, salt marsh, *Spartina*, tidal restoration, vegetation.

Introduction

For centuries, salt marsh ecosystems worldwide have been lost or severely degraded as a result of various human activities. In the United States, diking has resulted in the impairment of thousands of hectares of salt marsh (Tiner 1984). Diked marshes suffer from reduced salinities, altered porewater and soil chemistry, and peat subsidence. This is followed by the death of native halophytes and invasions of upland, freshwater, and/or exotic species (Roman et al. 1984; Sinicrope et al. 1990; Roman et al. 1995; Portnoy & Giblin 1997; Portnoy 1999; Warren et al. 2002).

Although tidal restoration projects are occurring with greater frequency, quantitative analyses of subsequent vegetation changes are limited. Moreover, plant community responses to tidal restoration can be quite disparate. For example, although salt-intolerant species generally decline quickly in response to tidal restoration (Burdick et al. 1997), they may persist at higher elevations (Barrett &

Niering 1993). Thus, topographic heterogeneity may contribute substantially to plant community development. Size also matters in that large sites tend to accumulate halophytes at a faster rate than smaller ones (Wolters et al. 2005b). The proximity of halophyte populations to the restoring system must be a critical factor as well because they are a source of seeds and propagules. Warren et al. (2002) summarized changes within six restored marshes in southern New England and found that the re-establishment of salt marsh plants was highly variable. Responses of key species like Common reed (*Phragmites australis*, hereafter referred to as *Phragmites*), the exotic haplotype (haplotype M from Eurasia) of which is an invasive species in North America, also can be inconsistent, exhibiting either increasing (Sinicrope et al. 1990) or decreasing trends (Roman et al. 2002; Buchsbaum et al. 2006). On a larger scale, the responses of *Phragmites* to seawater influence can even vary with local climatological factors (Lissner et al. 1999). Given the different trajectories that different systems may take, there is inherent value in reporting on tidal restoration projects as each case adds to our understanding about the process itself and the range of possible outcomes.

In Cape Cod (Massachusetts, U.S.A.), nearly 1,400 ha of salt marsh habitat have been diked over the past 350 years (Portnoy et al. 2003). More than half the affected area lies within the Cape Cod National Seashore (CCNS), including an approximately 40 ha tide-restricted portion of the Hatches Harbor marsh located at the northern tip

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of Cape Cod (Provincetown). This article summarizes vegetation changes that have taken place in this marsh since the onset of tidal restoration in 1999 and evaluates key environmental variables contributing to these changes. This restoration project differs from many others in that tidal flow was introduced incrementally over a period of 6 years rather than all at once. Flow was controlled by progressively increasing the cross-sectional area of openings within a restricting dike via adjustable tide gates, allowing for stepwise increases in seawater exchange.

Methods

Study Site

Hatches Harbor salt marsh is located at the northern end of Cape Cod in the town of Provincetown, Massachusetts (lat 42°03′55″N, long 70°14′09″W). In 1930, in an attempt to control nuisance mosquito populations, an earthen dike was constructed that severed approximately half the marsh from tidal influence (Fig. 1). Shortly thereafter, the Provincetown Municipal Airport was built within the diked floodplain. Hydrologic and biogeochemical changes that

occurred after the diking severely impacted the structure and function of the upstream marsh. Porewater salinities plummeted, allowing the establishment and expansion of freshwater wetland taxa, including invasive exotic plants like *Phragmites* and purple loosestrife (*Lythrum salicaria*). Prolonged dewatering of the marsh brought about an invasion of upland shrubs at higher elevations. These communities contrast sharply with the unrestricted marsh where the vegetation is dominated by smooth cordgrass (*Spartina alterniflora*) and salt meadow hay (*S. patens*).

The 1930 dike included a small (0.6 m diameter) culvert fitted with a one-way flap valve that allowed water upstream of the dike to drain out but prevented the entry of seawater. The flap valve was permanently removed during repair work to the dike in 1987, permitting limited seawater exchange and, consequently, some recolonization of creekbanks by *S. alterniflora*. However, the vast majority of the marsh remained dramatically altered from decades of hydrologic isolation. In 1997, the National Park Service, Provincetown Airport Commission, and Federal Aviation Administration developed a plan to construct a series of large culverts that would restore tidal function while protecting the adjacent airport from storm surges. In that
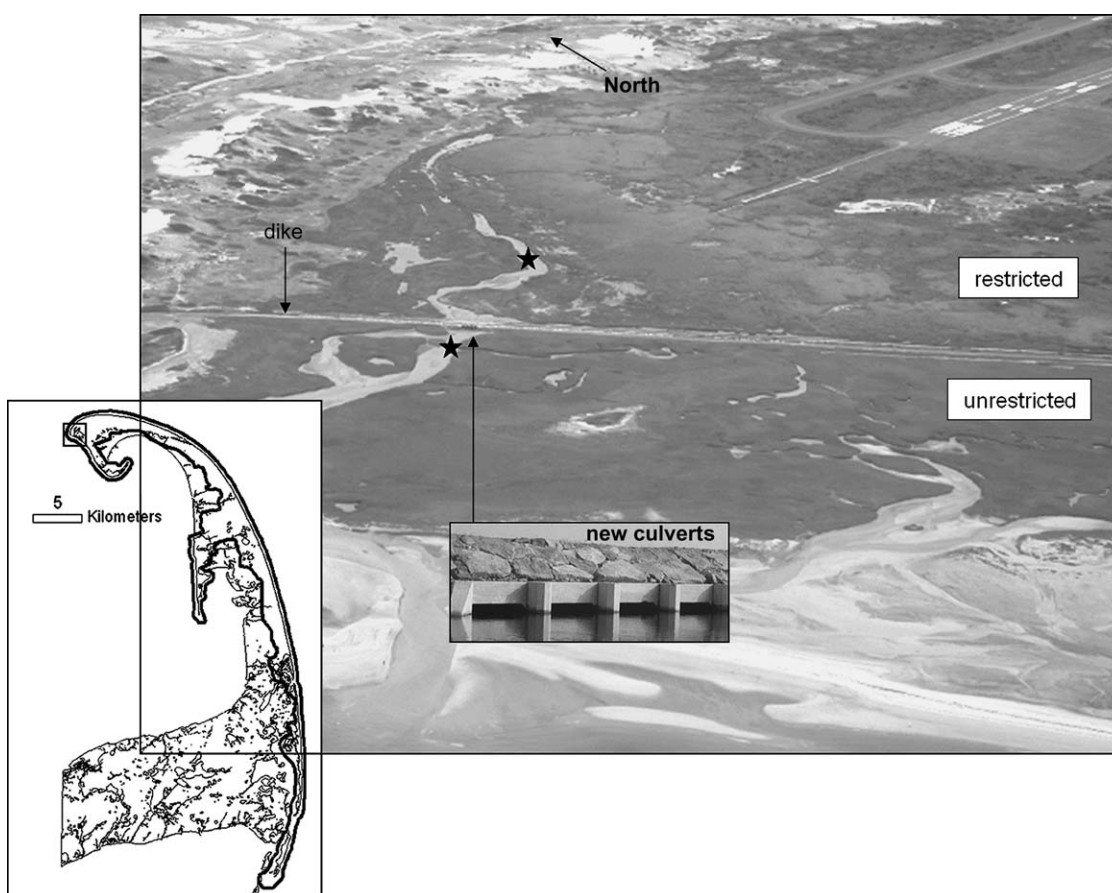
Figure 1. Map of lower Cape Cod and an oblique aerial photograph of the Hatches Harbor marsh in 2004. Locations of the water level recorders are indicated with star symbols and a photograph of the new culverts is provided.

same year, a network of permanent 1-m^2 sampling plots was established on the tide-unrestricted and tide-restricted sides of the dike to document plant community responses. In 1998, the existing 0.6-m culvert was replaced with four 2.1-m wide × 1-m high rectangular box culverts, each with an adjustable door to control flow. Since April 1999, seawater exchange through these culverts has been increased by incrementally raising these doors. In October 2005, the doors were opened fully to allow for maximum possible exchange.

Sampling Design

In 1997, permanent vegetation plots (1 m^2) were established along linear transects that were positioned by randomly selecting locations along the main tidal creek that runs southwest to northeast through the system. Along these transects, oriented perpendicular to the creek, the initial plots were placed randomly within the vegetated creekbank zone. The rest of the plots were established at regular intervals (20 m on the restricted side and 30 m on the unrestricted side) proceeding upslope from the creek. Transects 1–6 ($n = 133$) were located within the tide-restricted marsh, whereas transects 7–9 ($n = 57$) were placed in the tide-unrestricted marsh. Ground surface elevations at each plot were determined by laser leveling (TopCon ITS-1 Total Station).

Given the random nature for setting the transects and the large distance between plots, it can be assumed that the individual vegetation plots are independent (Elzinga et al. 2001). All plots (total = 190) were sampled in 1997. In 2002, 2004, and 2006, a subset of these plots ($n = 135$) were sampled based on a power analysis that suggested fewer plots were required for long-term monitoring (James-Pirri et al. 2007). In addition, a number of plots were eliminated due to various construction activities in the vicinity of the airport. Finally, some of the creek-edge plots established in 1997 eventually eroded away due to migration of the tidal channel. Disturbed or eroded plots were not assessed in later surveys. Thus, the final number of plots analyzed was 124 (98 tide restricted and 26 tide unrestricted)—all of which were surveyed in all 4 years.

Environmental Sampling

Beginning in 1998, YSI (model UPG6000; Yellow Springs, OH, U.S.A.) water level loggers were deployed seaward and landward of the dike during 16 November to 22 December 1998, 12 September to 2 October 2002, and 12 September to 2 October 2006 (Fig. 1). The loggers were set to record water levels every 15 minutes. In 2006, the YSI units were replaced with HOBO water level recorders. The pressure transducers in the loggers were referenced to NAVD 88 by differential leveling from local benchmarks.

Porewater was sampled in a subset of plots along a segment of transect 2 (0–240 m) in the tide-restricted marsh and transect 7 (0–300 m) in the tide-unrestricted side in 1997, 2000, 2001, 2002, 2003, 2004, and 2006. We refer to these as "index transects." In addition, porewater salinities were obtained for the entire set of tide-restricted plots in 2004 and 2006. No sampling was done along the tide-unrestricted index transect after 2003 based on the observation that there was extremely low variability in salinities and sulfide concentrations among years.

Porewater was collected at or near low tide and between mid-August and early-October to coincide with reported fall maximum sulfide concentrations in New England salt marshes (Howarth & Teal 1979). From 1997 to 2002, samples from both index transects were collected daily over the course of 7–9 days. These data were then averaged to obtain a single value per plot. From 2003 to 2006, sampling of the index transects was completed within a single day. Porewater was withdrawn from the sediment using a 2-mm internal diameter stainless steel probe with a slotted point. The probe was inserted 10 cm into the sediment, within the active root zone, and water was drawn into a 3-mL syringe fitted onto silicone tubing attached to the probe's upper end. Any air aspirated into the syringe was discharged prior to collecting a sample for sulfide analysis. If the peat water level was deeper than 10 cm from the surface, no sample was collected. All but 0.5 mL of sample contained in the syringe was discharged onto a refractometer (Vista Model A366ATC) to read salinity (± 1 ppt). The remaining 0.5 mL was discharged directly into a 20-mL scintillation vial containing 12 mL of 2% zinc acetate to precipitate sulfides. Total sulfides were then determined colorimetrically in the laboratory (Cline 1969).

Vegetation Sampling

Percent cover by species and other cover types (e.g., bare ground, wrack) was assessed using the point-intercept method (Roman et al. 2001) except in 2006, when cover was estimated by visual methods based on a modified Braun-Blanquet scale (0 = 0, >0–1% = 1, 2–5% = 2, 6–10% = 3, 11–25% = 4, 26–50% = 5, 51–75% = 6, and 76–100% = 7). To make comparisons among all years, the point-intercept data from 1997, 2002, and 2004 were transformed to their corresponding cover class values. Although there is the potential for some error to be introduced by switching methods, numerous studies have shown that visual assessments yield similar results when compared to the point-intercept technique (Poissonet et al. 1973; Smartt et al. 1974; Kent & Coker 1992). Also because the cover classes are quite broad, there is a relatively high level of certainty that the transformed point counts are appropriately represented within each class (Bråkenhielm & Qinghong 1995).

In addition to assessments of cover, *Phragmites* stem heights and stem densities within the vegetation plots were determined at the end of the growing season (September to October). In 1997, these data were collected

only along the tide-restricted index transect. In 2002, 2004, and 2006, all tide-restricted plots were surveyed. When densities were very high (>30 stems/m^2), a 0.25-m^2 subplot (the nearest bottom corner of the 1-m^2 plot) was used and the densities converted to stems/m^2. Using height and stem density values, *Phragmites* biomass (g/m^2) was then calculated based on the equations of Thursby et al. (2002).

Data Analysis

Nonmetric multidimensional scaling (NMDS), based on Bray–Curtis similarity matrices generated from cover scores, was used to illustrate similarities in species composition between the unrestricted and the restricted marsh areas over time (Primer ver. 5). Bray–Curtis distance measurements are considered more appropriate for analyzing species abundance data than Euclidean distances based on the treatment of zero values (Legendre & Gallagher 2001; McArdle & Anderson 2001). For some species within the same genus, where positive identification to species was uncertain, the midpoint percentages of the cover values for each species were summed to obtain a single value for the genus. These were then transformed back to the appropriate cover score. Where the sums of two or three species exceeded 100%, the upper limit value of the cover scale (7; 75–100%) was used. Combining of species was done for two blackberry (*Rubus*) species (*Rubus hispidus* and *R. flagellaris*), three goldenrod (*Solidago*) species (*Solidago rugosa*, *S. elliottii*, and *S. canadensis*), two flat-topped goldenrod (*Euthamia*) species (*Euthamia graminifolia* and *E. tenuifolia*), two sea blite (*Suaeda*) species (*Suaeda maritima* and *S. linearis*), and two skullcap (*Scutellaria*) species (*Scutellaria galericulata* and *S. lateriflora*).

Differences in plant communities between years or area of marsh (i.e., unrestricted vs. restricted) were tested by analysis of similarities (ANOSIM; Primer ver. 5) based on species cover scores (Webb et al. 2000; Clarke & Warwick 2001; Roman et al. 2002; Carlo & Giancarlo 2006; Clarke et al. 2006). Although the unrestricted marsh is not a perfect control site because it is not completely independent of changes in tidal flow through the dike, it represents the

desired condition. Also, hydrology on the downstream side of the restriction is overwhelmingly influenced by Cape Cod Bay where the tidal range is in excess of 3 m and freshwater discharge is trivial compared to the high-salinity tidal prism. This is demonstrated by the fact that water both flooding into and ebbing out of the restricted marsh has the same high salinity. Changes in the geomorphology of the tidal inlet can also have an effect, but both drown out any minor changes in tide dynamics in the unrestricted marsh caused by the dike opening. Moreover, it would be inappropriate to use other unrestricted marshes within CCNS for comparison because they are all quite different in terms of tidal range, elevation, sediment properties, water quality, and age.

Similarity percentages were calculated to examine the contribution of species to dissimilarity among groups (Primer ver. 5). Three-dimensional graphs of mean Bray–Curtis similarity values were plotted using Tablecurve 3d. Changes in the cover of individual species between 1997 and 2006 were tested by Wilcoxon signed rank tests for paired samples (Lehmann & D'Abrera 1975). However, cover scores were transformed to their midpoint percentages for presentation of mean values of individual species in the tables and figures. Porewater salinities and *Phragmites* biomass data were log-transformed and analyzed by repeated measures analysis of variance (ANOVA). Linear and nonlinear regressions were used to explore and test the significance of relationships between vegetation and environmental variables (Statistica ver. 6.0).

Results

Tide Heights

Tidal range for the unrestricted marsh ranged between 0.66 m in 1998 and 0.90 m in 2006 (Table 1). This variability is due to differences in the timing of deployment as well as changes in geomorphology of the system's tidal inlet to Cape Cod Bay, which can be substantial from year to year. Prior to restoration, tidal range of the restricted marsh was 0.26 m, just 39% of the range for the tide-unrestricted marsh (0.66 m). With progressive opening of

Table 1. Mean high and low water levels relative to mean sea level (NAVD 88) during periods of deployment throughout the study, tidal range, total cross-sectional area of open culverts, and % tidal range of unrestricted marsh.

	Mean High	Mean Low	Tidal Range	Area of Opening	% Tidal Range of Unrestricted Marsh
Unrestricted					
16 November 1998 to 22 December 1998	1.42	0.76	0.66		
12 September 2002 to 2 October 2002	1.72	0.83	0.88		
12 September 2006 to 2 October 2006	1.71	0.81	0.90		
Restricted					
16 November 1998 to 22 December 1998	1.29	1.04	0.26	0.29	39
12 September 2002 to 2 October 2002	1.60	1.04	0.56	3.41	63
12 September 2006 to 2 October 2006	1.59	1.04	0.55	7.79	61

the structure, tidal range of the restricted marsh increased to 61–63% of the tide-unrestricted range. By 2006, the tide-restricted marsh had experienced a more than 50% increase in tidal range. This gain is due to increasing high tide heights, given that low tides did not change.

Porewater Chemistry

From 1997 to 2003, salinities in the unrestricted marsh did not exhibit any statistical change, averaging 32 ppt with very little variation among years (SE = 0.2 or 0.063% of the mean; data not shown). As expected, plots along the tide-restricted index transect changed dramatically with tide restoration (repeated measures ANOVA, $F = 12.6$, $p \leq 0.001$), showing progressive increases each year with the greatest magnitude of change occurring between 1997 and 2002 and at plots greater than 80 m from the tidal creek (Fig. 2). In 1997, only one plot along the tide-restricted transect had a salinity value greater than 25 ppt, whereas in 2006, all plots were greater than 25 ppt and most were near 30 ppt. In 2006, abrupt reductions in salinity occurred closer to the tidal creek in transects further from the dike (Fig. 5b).

Prior to 2002, total dissolved sulfides were consistently low, falling below 20 μM throughout both sides of the wetland (Table 2). In 2002, sulfide concentrations increased substantially along the tide-unrestricted index transect, especially at vegetation plots distant from the tidal creek. In 2003, concentrations were high along both tide-unrestricted and tide-restricted index transects. This is likely due to tide levels in both 2002 and 2003 being higher than in previous sampling periods, which would limit drainage of the peat. Notwithstanding, sulfide concentrations were still less than 60 μM, which is very low for salt marshes in this region (Teal & Howes 1996, Portnoy & Valiela 1997). This reflects the high permeability and, thus, efficient regular low tide drainage and aeration of the sandy peat within this system.

Vegetation

Of the total number of taxa recorded in 1997, approximately two-thirds declined in cover and frequency with tide restoration (Table 3). This group comprises mainly freshwater (i.e., salt intolerant) wetland and upland plants. meadowsweet (*Spiraea* spp.), blackberry (*Rubus*) spp., saltmeadow rush (*Juncus gerardii*), northern bayberry (*Morella pensylvanica*), and marsh fern (*Thelypteris palustris*) exhibited the largest reductions in cover. *Rubus* spp., purple loosestrife (*Lythrum salicaria*), *M. pensylvanica*, slender goldenrods (*Euthamia* spp.), and sedges (*Carex* spp.) showed the greatest reductions in frequency. Given that *L. salicaria* is a highly invasive plant in North America, its decline is a noteworthy benefit of tidal restoration. Saltmeadow rush (*J. gerardii*), a high marsh species intolerant of full-strength seawater, completely disappeared (note, however, that this species is not present in the unrestricted marsh). In contrast, the cover of native halophytes greatly increased from 1997 to 2006, with perennial glasswort (*Salicornia virginica*) and *Spartina alterniflora* showing the largest increases in cover and frequency (Table 3). The cover and frequency of *Phragmites* remained unchanged.

Separation of the 1997, 2002, 2004, and 2006 tide-restricted plant communities in three-dimensional space (NMDS of Bray–Curtis values) shows the magnitude of change that has occurred over time (Fig. 3). Species composition in the tide-restricted marsh in any given year was significantly different from any other year, except between 2004 and 2006. Several species contributed to most of the observed changes over the entire duration of the study (i.e., between 1997 and 2006) for the tide-restricted marsh. *Phragmites* accounted for the most dissimilarity (10.5%), which was primarily related to a shift in its distribution (Table 4). Other species that contributed were *S. alterniflora*, which increased in abundance, and *J. gerardii*, *M. pensylvanica*, and *Rubus* spp, all of which declined. Despite the shift toward more salt-tolerant species within
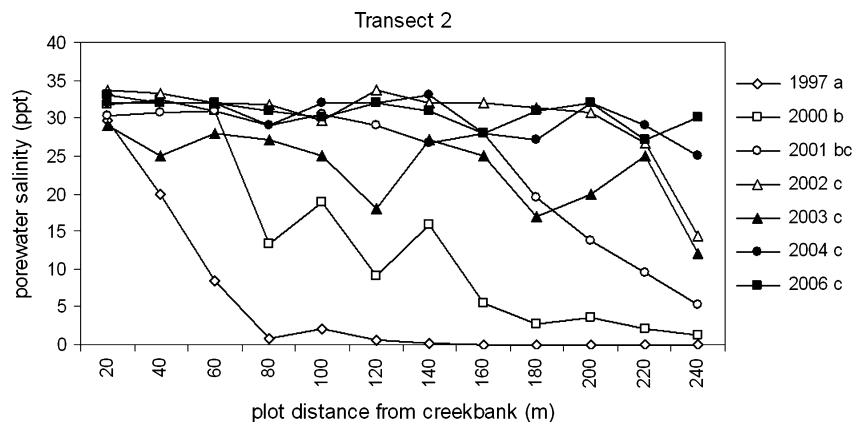

Figure 2. Porewater salinities along the tide-restricted index transect by year (letters to the right of the legend labels indicate statistical separation of mean values for each year; those sharing the same letter are statistically equal).

Table 2. Mean porewater sulfide concentrations (μM) for each index transect and year.

Transect	1997	1999	2000	2001	2002	2003
2 (restricted)	3.97 (12)	3.93 (12)	4.08 (12)	0.42 (12)	1.18 (12)	15.62 (12)
7 (unrestricted)	5.13 (13)	3.08 (13)	No data	7.34 (8)	18.90 (11)	20.36 (11)

Values given in parentheses are number of replicate plots.

the tide-restricted marsh, there was still a significant dissimilarity between it and the tide-unrestricted marsh (ANOSIM global $R = 0.18$, $p \leq 0.001$). Species composition in the unrestricted marsh varied only slightly from year to year and remained statistically stable (ANOSIM global $R = 0.013$, $p = 0.21$).

Although a portion of the vegetation of the tide-restricted marsh now bears a greater resemblance to the unrestricted side, in their entirety the two areas remain quite different. Some plots have changed substantially, whereas others have shown very little or no change. Regression analysis showed that the spatial component of change is best related to elevation (exponential; $R^2 = 0.45$, $p \leq 0.001$). More specifically, plots at lower elevations had smaller differences between their Bray–Curtis values and the mean Bray–Curtis value for all unrestricted plots. Similarity was also significantly correlated with distance from culverts (linear; $R^2 = 0.40$, $p \leq 0.001$) and porewater salinities (logarithmic; $R^2 = 0.27$, $p \leq 0.001$). Multiple regression using all three variables produced the highest coefficient of determination (linear; $R^2 = 0.60$, $p \leq 0.001$, $y = 1.65$ [elevation in meters] $+ 0.001$ [distance in meters] $- 0.021$ (salinity in ppt)] (Fig. 4).

Trends in Key Species

Since 1997, the number of plots containing *S. alterniflora* has more than tripled (Table 5). In addition, its distribution has expanded a considerable distance upslope (80–260 m) from the main tidal creek (Table 5). The frequency of *S. patens* changed little, although it ranged farther into the marsh, while retreating from lower elevations. Other native halophytes such as sea blites (*Suaeda* spp.) and glassworts (*Salicornia* spp.) also exhibited rapid increases over this time period. In contrast, spikegrass (*Distichlis spicata*) expanded to a much lesser extent (Table 3).

Phragmites was present in more plots in 2006 than in 1997 and its mean biomass increased from 2002 to 2006, but the difference was not statistically significant (repeated measures ANOVA; $F = 1.97$, $p = 0.4$) (Table 5). It is primarily the distribution of *Phragmites* within the marsh that has changed most dramatically. *Phragmites* has shifted far upslope toward the wetland periphery and away from the main tidal creek (Fig. 5a). *Phragmites* biomass increased with distance away from the culverts (power; $R^2 = 0.29$, $p \leq 0.001$) and was negatively correlated with 2006 porewater salinities (linear; $R^2 < 0.12$, $p = 0.01$), although the latter relationship was weaker. Notwithstanding, where salinities are roughly between 10 and 25 ppt, this species is thriving (Fig. 5b). In contrast, where salinities are greater than 25 ppt, *Phragmites* is greatly diminished or has disappeared altogether. There was no significant relationship with elevation (power; $R^2 = 0.09$, $p = 0.11$).

Discussion

After 7 years of progressively increasing seawater flow through the Hatches Harbor dike, there have been significant physicochemical and floristic changes in the tide-restricted marsh. Overall, a 22% increase in tidal range was facilitated by the new culvert system. Although this seems rather small given the nearly 27-fold increase in the cross-sectional area of the dike opening, it translates to a very large volume of water being spread out over a much greater area of marsh. The area of *Spartina*-dominated salt marsh vegetation in the tide-restricted marsh has expanded well beyond the estimated 5 ha that existed in 1995 (Portnoy et al. 2003). With the exception of *Puccinellia distans*, which disappeared, the restricted side of Hatches Harbor has attained all species present in the unrestricted side within 7 years.

The degree to which species composition in the tide-restricted marsh resembled the tide-unrestricted marsh was most closely related to elevation and distance from the point of seawater entry (i.e., the culverts), both of which determine flood duration and long-term porewater salinity conditions. Confounding these relationships are areas of isolated higher elevation "islands" in relatively close proximity to the culverts that support upland taxa as well as depressions in the interior marsh where salinities are still low enough for freshwater species.

The relationship between species composition and porewater salinity was weaker than that observed for either elevation or distance from the culverts, presumably because species changes lag behind changes in physicochemical conditions. Thus, the current vegetation most likely reflects the duration over which certain salinity levels have prevailed at each plot rather than being indicative of the most recently measured values. However, all three variables (elevation, distance from culverts, and porewater salinity) together explained quite well the extent to which tide-restricted plots resemble the tide-unrestricted community. Porewater sulfide presumably played a relatively minor role in influencing vegetation as concentrations were low. Such conditions demonstrate the excellent drainage that the culvert system now permits and the sandy, low organic content sediments that allow the entry of air into the root zone at low tide.

Table 3. Mean cover (%) and frequency of species by year for the tide-restricted marsh ("E" indicates exotic taxa) and corresponding change between 1997 and 2006.

Species	Typical Habitat	Mean Cover (%)					Frequency				
		1997	2002	2004	2006	Change	1997	2002	2004	2006	Change
Spiraea spp.	FW	21.84	5.48	5.87	0.37	−21.48*	0.311	0.175	0.136	0.039	−0.272
Rubus spp.	FW, UPL	20.00	11.13	7.79	1.01	−19.00*	0.447	0.272	0.204	0.058	−0.388
Juncus gerardii	BR	14.23	7.06	0.00	0.00	−14.23*	0.243	0.107	0.000	0.000	−0.243
Morella pensylvanica	FW, UPL	14.33	4.97	3.17	2.33	−12.00*	0.379	0.223	0.214	0.078	−0.301
Thelypteris palustris	FW	9.77	4.44	3.79	0.42	−9.35*	0.252	0.087	0.078	0.039	−0.214
Deschampsia flexuosa	UPL	9.35	4.65	3.26	1.83	−7.52*	0.146	0.107	0.058	0.058	−0.087
J. effusus	FW	6.41	1.36	0.77	0.26	−6.16*	0.223	0.078	0.068	0.049	−0.175
Baccharis halimifolia	BR, SM	6.04	0.93	0.00	0.00	−6.04*	0.223	0.058	0.000	0.000	−0.223
Toxicodendron radicans	FW, UPL	6.43	2.14	1.67	0.69	−5.74*	0.243	0.136	0.107	0.039	−0.204
Rosa spp.	FW	6.09	2.57	1.67	0.52	−5.57*	0.262	0.194	0.087	0.029	−0.233
Carex spp.	FW	5.39	1.16	0.42	0.14	−5.25*	0.320	0.068	0.049	0.049	−0.272
Euthamia spp.	FW	6.01	1.15	3.21	0.99	−5.02*	0.388	0.087	0.204	0.107	−0.282
Holcus lanatus (E)	UPL	5.01	1.49	0.71	0.24	−4.77*	0.233	0.107	0.058	0.039	−0.194
Lythrum salicaria (E)	FW, BR	4.62	0.65	0.51	0.22	−4.40*	0.417	0.087	0.068	0.049	−0.369
Scirpus cyperinus	FW, BR	3.80	0.52	1.51	0.17	−3.63*	0.184	0.029	0.058	0.019	−0.165
Symphyotrichum novi-belgii	UPL	3.67	1.48	1.94	0.13	−3.53*	0.320	0.117	0.165	0.087	−0.233
Agrostis stolonifera	FW	3.35	0.00	0.00	0.00	−3.34	0.097	0.000	0.000	0.010	−0.087
Eupatorium dubium	FW	3.06	0.90	0.57	0.00	−3.06*	0.126	0.078	0.049	0.010	−0.117
Onoclea sensibilis	FW	2.45	0.24	0.29	0.00	−2.44*	0.117	0.019	0.049	0.010	−0.107
Solidago spp.	FW	2.00	3.94	0.54	0.17	−1.83*	0.204	0.252	0.039	0.010	−0.194
Spiraea tomentosa	FW	1.77	0.58	0.70	0.00	−1.77*	0.117	0.049	0.078	0.000	−0.117
J. canadensis	FW	1.32	0.28	0.42	0.04	−1.28*	0.087	0.039	0.058	0.019	−0.068
Fragaria virginiana	FW	1.25	0.00	0.00	0.00	−1.25	0.126	0.000	0.000	0.000	−0.126
Vaccinium macrocarpon	FW	1.84	1.29	2.35	0.73	−1.11	0.049	0.078	0.087	0.058	0.010
Spartina patens	SM	6.09	6.00	6.80	5.19	−0.90	0.136	0.146	0.184	0.146	0.010
Typha angustifolia	FW, BR	0.87	0.01	0.00	0.00	−0.87*	0.078	0.019	0.000	0.000	−0.078
Scheonoplectus pungens	FW, BR	1.87	0.97	1.46	1.04	−0.83	0.068	0.039	0.039	0.049	−0.019
Lycopus spp.	FW	0.77	0.04	0.11	0.00	−0.77*	0.078	0.029	0.039	0.000	−0.078
A. hyemalis	FW	0.73	0.00	0.00	0.00	−0.73	0.087	0.000	0.000	0.000	−0.087
Parthenocissus quinquefolia	UPL	0.73	0.00	0.03	0.00	−0.73	0.019	0.000	0.010	0.000	−0.019
Triadenum virginicum	FW	0.69	0.31	0.39	0.05	−0.64*	0.097	0.058	0.068	0.039	−0.058
Ammophila breviligulata	UPL	1.35	1.77	1.49	0.80	−0.55*	0.049	0.049	0.049	0.029	−0.019
Viburnum dentatum	FW	0.54	0.00	0.00	0.00	−0.54*	0.039	0.000	0.010	0.000	−0.039
Photinia spp.	FW, UPL	0.35	0.35	0.50	0.00	−0.35	0.019	0.019	0.049	0.000	−0.019
V. corymbosum	FW	0.49	0.17	0.73	0.17	−0.32	0.019	0.010	0.049	0.010	−0.010
Puccinellia distans	BR, SM	0.31	0.00	0.00	0.00	−0.31	0.039	0.000	0.000	0.000	−0.039
Ilex verticillata	FW	0.51	1.21	1.45	0.24	−0.28	0.058	0.039	0.068	0.029	−0.029
Polygonella articulata	UPL	0.28	0.00	0.03	0.03	−0.24	0.029	0.000	0.010	0.010	−0.019
Chenopodium album	UPL	0.24	0.00	0.00	0.00	−0.24	0.019	0.000	0.000	0.000	−0.019
Achillea millefolium	UPL	0.22	0.03	0.07	0.00	−0.21	0.029	0.010	0.010	0.010	−0.019
Rosa rugosa (E)	UPL	0.20	0.11	0.07	0.00	−0.20	0.019	0.029	0.010	0.000	−0.019
Galium trifidum	FW	0.18	0.00	0.00	0.00	−0.18	0.029	0.000	0.000	0.000	−0.029
Panicum lanuginosum	UPL	0.18	0.00	0.00	0.00	−0.18	0.029	0.000	0.000	0.000	−0.029
Teucrium canadense	FW	0.17	0.00	0.00	0.00	−0.17	0.010	0.000	0.000	0.000	−0.010
Osmunda regalis	FW	0.32	0.49	0.49	0.15	−0.17	0.010	0.019	0.019	0.029	0.019
A. perennans	UPL	0.11	0.00	0.00	0.00	−0.11	0.019	0.000	0.000	0.000	−0.019
Lactuca canadensis	UPL	0.10	0.00	0.00	0.00	−0.10	0.029	0.000	0.000	0.000	−0.029
Rhus copallina	UPL	0.14	0.82	0.72	0.04	−0.10	0.029	0.078	0.058	0.019	−0.010
Schizachyrium scoparium	UPL	0.07	0.03	0.00	0.00	−0.07	0.010	0.010	0.000	0.000	−0.010
Scutellaria spp.	FW	0.07	0.04	0.00	0.00	−0.07	0.019	0.019	0.010	0.000	−0.019
Sisyrinchium atlanticum	UPL	0.07	0.00	0.00	0.00	−0.07	0.019	0.000	0.000	0.000	−0.019
Artemisia stellariana	UPL	0.03	0.00	0.00	0.00	−0.03	0.010	0.000	0.000	0.000	−0.010
Epilobium leptophyllum	UPL	0.03	0.00	0.00	0.00	−0.03	0.010	0.000	0.000	0.000	−0.010
Festuca rubra	UPL	0.03	0.00	0.00	0.00	−0.03	0.010	0.000	0.000	0.000	−0.010
Habenaria clavellata	FW	0.03	0.00	0.00	0.00	−0.03	0.010	0.000	0.000	0.000	−0.010
Hieracium spp.	UPL	0.03	0.00	0.03	0.00	−0.03	0.010	0.000	0.010	0.000	−0.010
Hudsonia tomentosa	UPL	0.03	0.00	0.00	0.00	−0.03	0.010	0.000	0.000	0.000	−0.010
Ribes lacustre	FW	0.03	0.00	0.00	0.00	−0.03	0.010	0.000	0.000	0.000	−0.010

Table 3. Continued

Species	Typical Habitat	Mean Cover (%)					Frequency				
		1997	2002	2004	2006	Change	1997	2002	2004	2006	Change
Viola lanceolata	FW	0.03	0.00	0.00	0.00	−0.03	0.010	0.000	0.000	0.000	−0.010
Amelanchier spp.	FW, UPL	0.00	0.03	0.00	0.00	0.00	0.000	0.010	0.000	0.000	0.000
A. campestris	UPL	0.00	0.11	0.00	0.00	0.00	0.000	0.029	0.000	0.000	0.000
Boehmeria cylindrica	FW	0.00	0.15	0.00	0.00	0.00	0.000	0.019	0.000	0.000	0.000
Dicanthelium spp.	UPL	0.00	0.00	0.00	0.00	0.00	0.000	0.000	0.010	0.000	0.000
Drosera rotundifolia	FW	0.00	0.00	0.04	0.00	0.00	0.000	0.000	0.019	0.000	0.000
Eleocharis tenuis	FW	0.00	0.00	0.03	0.00	0.00	0.000	0.000	0.010	0.000	0.000
Gaylussacia baccata	UPL	0.00	0.03	0.00	0.00	0.00	0.000	0.010	0.000	0.000	0.000
H. ericoides	UPL	0.00	0.17	0.00	0.00	0.00	0.000	0.010	0.000	0.000	0.000
J. greenii	FW	0.00	0.00	0.17	0.00	0.00	0.000	0.000	0.010	0.000	0.000
Lathyrus japonicus	UPL	0.00	0.00	0.03	0.00	0.00	0.000	0.000	0.010	0.000	0.000
Lechea maritima	UPL	0.00	0.03	0.00	0.00	0.00	0.000	0.010	0.000	0.000	0.000
Plantago spp.	UPL	0.00	0.03	0.00	0.00	0.00	0.000	0.010	0.000	0.000	0.000
Prunus serotina	UPL	0.97	0.32	1.46	0.97	0.00	0.019	0.019	0.019	0.019	0.000
Rumex orbiculatus	FW	0.00	0.00	0.00	0.00	0.00	0.000	0.010	0.000	0.000	0.000
Salix bebbiana	FW	0.00	0.00	0.32	0.00	0.00	0.000	0.000	0.010	0.000	0.000
Smilax rotundifolia	FW, UPL	0.00	0.00	0.00	0.00	0.00	0.000	0.010	0.000	0.000	0.000
V. angustifolium	UPL	0.00	0.32	0.00	0.00	0.00	0.000	0.029	0.000	0.000	0.000
R. acetosella (E)	UPL	0.00	0.35	0.04	0.03	0.03	0.000	0.029	0.019	0.010	0.010
Solidago sempervirens	UPL	0.28	0.07	0.25	0.32	0.04	0.029	0.019	0.029	0.010	−0.019
Limonium carolinianum	SM	0.03	0.00	0.12	0.12	0.08	0.010	0.000	0.039	0.039	0.029
Atriplex hastata	SM	0.00	0.00	0.09	0.18	0.18*	0.000	0.000	0.039	0.049	0.049
P. maritima	UPL	0.00	0.35	0.17	0.32	0.32	0.000	0.019	0.010	0.010	0.010
Phragmites australis (E)	FW, SM	22.02	18.77	20.25	23.04	1.02	0.485	0.563	0.563	0.534	0.049
Suaeda spp.	SM	0.00	0.24	3.39	1.13	1.13*	0.000	0.087	0.262	0.136	0.136
Distichlis spicata	SM	1.45	0.80	3.40	2.89	1.44	0.068	0.010	0.058	0.068	0.000
Salicornia maritima	SM	0.07	0.59	1.34	2.08	2.01*	0.019	0.136	0.243	0.155	0.136
S. alterniflora	SM	6.80	6.92	7.55	9.17	2.37*	0.097	0.107	0.194	0.301	0.204
S. virginica	SM	0.00	0.00	0.70	3.64	3.64*	0.000	0.000	0.107	0.146	0.146

Asterisks indicate significant difference ($p \leq 0.05$) in cover between 1997 and 2006. "Typical habitat" designations indicate where species are most commonly found in New England. FW, freshwater marsh; BR, brackish marsh; SM, salt marsh; UPL, upland.

The trajectory of key plant species has been quite variable. Predictably, freshwater taxa have declined, following a pattern very similar to other tide-restored marshes in New England (Roman et al. 2002; Buchsbaum et al. 2006). However, the salt marsh species *Juncus gerardii*, *P. distans*, and saltbush (*Baccharis halimifolia*) also were lost. This is presumably due to the hydrologic changes exceeding the ability of these species to migrate upslope. The above taxa are not tolerant of full-strength salinities and prolonged inundation and were apparently unable to shift their distribution fast enough to keep pace with the rising tide levels. In addition, seed dispersal, seed banks, and/or germination conditions were apparently inadequate for establishment elsewhere in the marsh.

It is primarily the growth of *Spartina alterniflora* that is responsible for the large increase in salt marsh vegetation upstream of the dike. Although *S. patens* also increased, it did not expand in the same manner as *S. alterniflora*. This may be due to the low abundance of *S. patens* in the tide-restricted marsh prior to restoration and/or the large distance between the location of *S. patens* in the unrestricted marsh and the culverts through which seeds could pass.
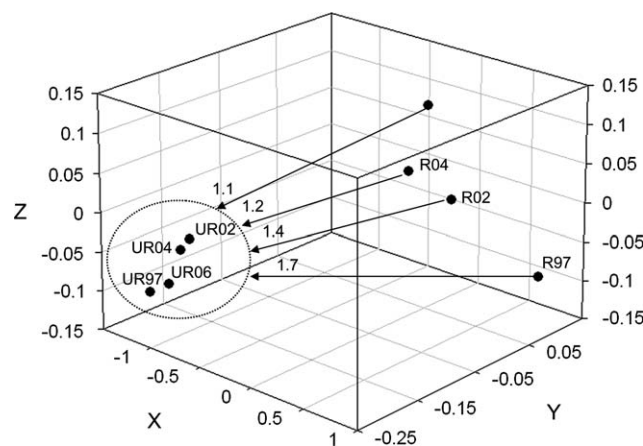

Figure 3. Three-dimensional graph of mean Bray–Curtis values in the tide-unrestricted versus -restricted marsh areas in 1997, 2002, 2004, and 2006. Points more similar to each other in community composition appear closer together (R, restricted marsh; UR, unrestricted marsh; and numbers beside labels denote last two digits of the year). Numbers above the arrows indicate the differences between mean Bray–Curtis similarity values of tide-restricted plots (each year) and tide-unrestricted plots (all years pooled).

Table 4. ANOSIM and SIMPER statistics for year to year comparisons of taxonomic composition within the tide-restricted marsh.

	ANOSIM		*SIMPER*	
	R Statistic	*p*	*Species*	*% Contribution*
1997 vs. 2002	0.057	≤0.001	*Phragmites australis*	10.5
1997 vs. 2004	0.141	≤0.001	*Spartina alterniflora*	6.6
1997 vs. 2006	0.180	≤0.001	*Juncus gerardii*	6.5
2002 vs. 2004	0.023	0.007	*Rubus* spp.	5.4
2002 vs. 2006	0.045	0.002	*Morella pensylvanica*	5.1
2004 vs. 2006	0.008	0.122		

SIMPER, similarity percentages.

Both would result in relatively small amounts of seed reaching suitable new habitat. It may also be due to the incremental method of tidal restoration. *Spartina alterniflora* is much more tolerant of flooding than *S. patens* (Naidoo et al. 1992). Consequently, this species was able to persist at the lowest elevations throughout the changing hydrologic regime while simultaneously expanding into higher elevations. Although *S. patens* colonized higher elevations as tide heights increased with each successive opening of the gates, it was forced to retreat from lower ones as it was unable to withstand longer periods of inundation (Burdick & Mendelssohn 1987, 1990). Finally, many areas with suitable hydrology (at higher elevations) for *S. patens* are still occupied by dense *Phragmites*, which further limits its establishment.

In contrast to the response of halophytic and salt-intolerant species, increased seawater exchange altered the distribution, more than the overall abundance, of *Phragmites*. The bulk of the *Phragmites* population has been able to shift position and stay within a zone of intermediate salinities (roughly 10–25 ppt) that has shifted upslope with each incremental opening of the culverts. These salinities are high enough to kill salt-intolerant taxa but are well within the tolerance range of *Phragmites* (Matoh et al. 1988; Hellings & Gallagher 1992; Lissner & Schierup 1997; Vasquez et al. 2006). As a result, *Phragmites* has invaded places where it was formerly absent. On a smaller scale, this was observed by Buchsbaum et al. (2006) following tidal restoration of a marsh in Ipswich, Massachusetts. In Hatches Harbor, *Phragmites* was killed
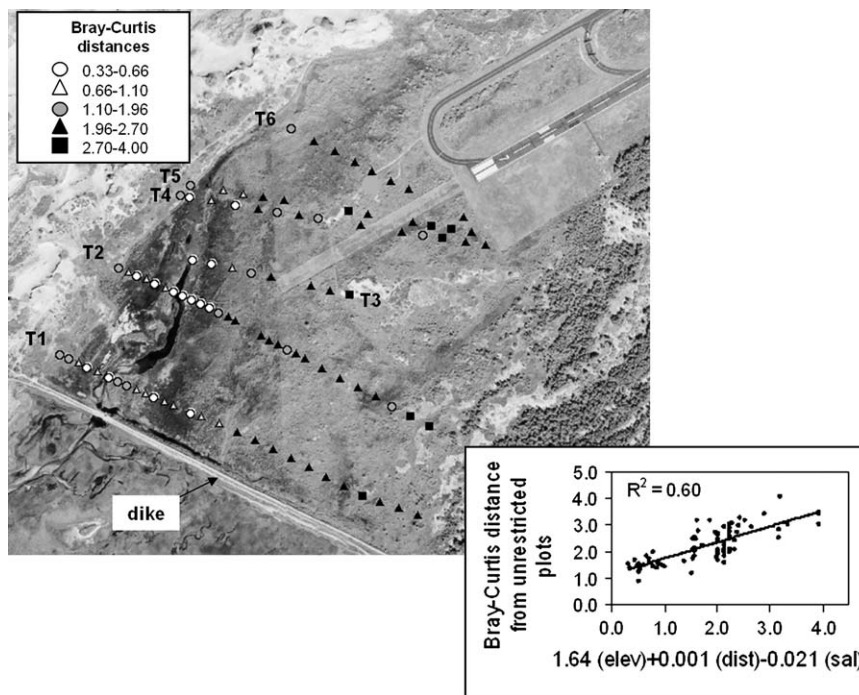

Figure 4. Map of tide-restricted vegetation plots depicting plant community similarity (Bray–Curtis distances) between each tide-restricted plot and the unrestricted plots (all plots pooled) in 2006. Smaller Bray–Curtis values indicate greater similarity to the tide-unrestricted vegetation. The inset graph shows the relationship between Bray–Curtis distances and values calculated from a best fit multiple regression equation that combines elevation, distance from culverts, and salinity for the most recent sampling year (2006).

Table 5. Frequency and distribution of *Spartina alterniflora* and *S. patens* and frequency and biomass of *Phragmites australis* in the tide-restricted marsh by year.

Species	Parameter	Transect	1997	2002	2004	2006
S. alterniflora	Frequency	1–6	0.097	0.107	0.165	0.311
	Distribution	1	0	0	140	260
		2	0	0	40	60
		3	0	0	40	80
		4	0	0	80	80
		5	0	0	40	80
		6	0	0	0	0
S. patens	Frequency	1–6	0.146	0.136	0.194	0.165
	Distribution	1	40	60	60	60
		2	0	20	60	80
		3	0	0	80	80
		4	160	160	240	240
		5	200	200	240	240
		6	0	40	40	40
P. australis	Frequency	1–6	0.456	0.505	0.563	0.563
	Biomass (g/m^2)	1–6	No data	597 (117)	558 (98)	808 (119)

Frequency is the number of plots with the species present/total number of plots. Distribution represents the greatest distance (m) from the tidal creek along each transect that the species was found. Numbers in parentheses beside *Phragmites* biomass values are standard errors of the means.

or stunted and sparse where porewater salinities were greater than 30 ppt. Because porewater sulfide concentrations were very low compared to what this species can withstand (Hotes et al. 2005), osmotic stress, rather than sulfide toxicity, accounts for its decline in these areas.

Despite the general trends mentioned above, *Phragmites* biomass was weakly correlated with elevation and porewater salinity. With respect to the former, many of the higher elevations in the marsh are still occupied by upland vegetation. For the latter, there are several
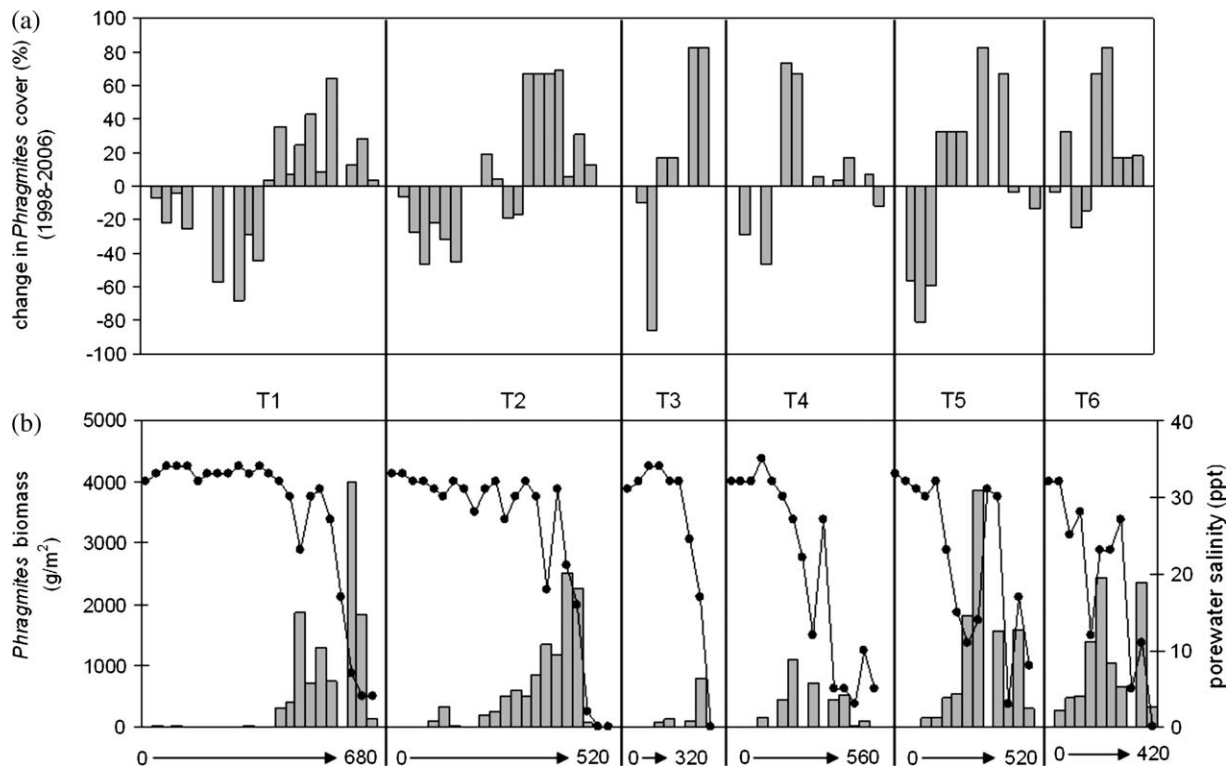

Figure 5. Changes in (a) *Phragmites* cover (%) between 1998 and 2006 and (b) *Phragmites* biomass distribution (histograms) relative to porewater salinity (line graph) in 2006 (numeric ranges show plot distances from main tidal creek by transect; T1–T6 indicate transect numbers).

plausible explanations. First, salinity is an instantaneous measure that does not necessarily represent long-term conditions in the root zone. Second, *Phragmites* vigor at a particular location may be confounded by clonal integration, which allows internal resources to be shared via an extensive network of rhizomes (Amsberry et al. 2000). As such, the vigor of *Phragmites* in high-salinity areas may be bolstered by the translocation of carbohydrates from individuals growing in more suitable conditions some distance away. Third, the salinity tolerance of this species is rather broad, adding considerable scatter to the regression. Another possibility is that many of the lower values of *Phragmites* biomass are indicative of plots that have been only recently invaded. Growth at very low salinities also could have been limited by competition from freshwater species (Amsberry et al. 2000).

Although incremental restoration allowed the tide-restricted marsh to adjust biologically and chemically to the reintroduction of seawater, it also provided *Phragmites* the opportunity to slowly grow away from unfavorable conditions and stay within a salinity range of 10–25 ppt. This species has the ability to spread rapidly by means of prostrate stems that creep into areas of salt-killed vegetation. In hindsight, fully opening the tide gates all at once may have thwarted this migration because growth would have been inhibited throughout the entire extent of the *Phragmites* population. In fact, this may be the preferred strategy for some restoration projects where *Phragmites* control is a primary objective. However, incremental restoration was prescribed for Hatches Harbor to maintain physical processes that would encourage salt marsh community development. If all the culverts were fully opened at the very beginning, much larger areas of barren mudflats would have been created by the rapid mortality of salt-intolerant vegetation and native halophytes may not have become established fast enough to revegetate this bare ground. Subsequently, sediment erosion could have altered marsh topography (i.e., elevation lowering) in a way that slowed or inhibited the revegetation process. In addition, there were concerns that a permanently flooded "lake" could have been created as a result of the subsidence that had occurred during the period of restriction. Finally, airport officials would only agree incremental openings because airport flooding was a major issue (Portnoy et al. 2003). Treating the leading edge of *Phragmites* with herbicide could prevent its spread upstream or upslope during incremental restoration. In fact, Greenwood and MacFarlane (2006) suggested both herbiciding and timing of restoration relative to seed bank depletion as a means to control *Phragmites* in Australia.

Further development of the salt marsh community upstream of the dike appears to be limited by the inability of seeds/propagules to move beyond the physical barrier of standing dead (salt killed) vegetation (Smith 2007). In their analysis of seed dispersal, Levine and Murrell (2003) suggest that the distribution of plant species is frequently regulated by factors that inhibit movement. Similarly, Wolters et al. (2005*a*) pointed out the importance of seed

sources and dispersal in northwestern Europe. At Hatches Harbor, dead stems of *Phragmites* and woody shrubs trap wrack material and prevent the dispersal of seeds across a large portion of the tide-restricted marsh. Standing dead vegetation may also affect the dynamics of water flow through the marsh and, therefore, influence flood duration and/or salinity. As this dead plant material degrades, further shifts in vegetation are expected as seeds and propagules are able to penetrate further into the marsh.

Given that seed dispersal dynamics and a variety of other physical, chemical, and biological process will continue to change, the present vegetation at Hatches Harbor does not represent an end point to the restoration. In Connecticut, some marshes still have not reached a steady state more than two decades after the onset of restoration (Warren et al. 2002). Onaindia et al. (2001) found that 35 years of natural recovery in salt marshes along the coast of Spain was not enough time for plant communities to become statistically similar to reference systems. Barrett and Niering (1993) estimated that only 28% of a tide-restricted marsh in the Barn Island Wildlife Management Area (Connecticut) had been restored because tidal flow was reintroduced 15 years earlier. Thom et al. (2002) predicted that full recovery of a diked marsh in Washington would take up to 75–150 years. Taken as a whole, the vegetation community of the tide-restricted side of the Hatches Harbor marsh is still very different from the tide-unrestricted marsh. Although the expectation is for further convergence, total restoration of the entire tide-restricted marsh is unrealistic because the dike still remains and now functions to protect the airport from flooding. However, the Hatches Harbor tidal restoration project has succeeded in returning a sizeable portion of degraded, fresh-, and brackish water wetland to a *Spartina*-dominated salt marsh plant community.

Implications for Practice

- The decline of salt-intolerant taxa is, not surprisingly, rapid. However, the expansion of native halophytes is much slower and quite variable among species.
- The recovery of salt marsh plant communities during tidal restoration can have a strong spatial component that is closely related to elevation, salinity, and distance from the point of seawater entry into the tide-restricted system.
- Incremental increases in tidal flow over a long period of time may not reduce the system-wide abundance of *Phragmites* because this species is able to migrate, through vegetative growth, away from stressful growing conditions.

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